FUNGAL PATHOGENS OF SPIDERS

H C EVANS

CAB International Institute of Biological Control, Silwood Park, Ascot, Berks SL5 7PY, UK

AND R A SAMSON

Centraalbureau voor Schimmelcultures, P.O. Box 273, 3740 AG Baarn, The Netherlands

This article deals exclusively with those fungi which are proven or purported pathogens of spiders (Araneae, Arachnida). They are usually included within the umbrella terms of entomo-genous or entomopathogenic fungi (Evans, 1982; Samson et al., 1987), since they share a similar morphology and biology with some groups of insect pathogens. Purists may argue for more precise teminology, such as *araneo-genous* or *araneopathogenic fungi*, to readily identify the pathogen-host associations involved. Indeed, many of the mycologists mentioned in the following pages have been guilty of confusing spiders with insects in their publications and all, including the present authors, have paid sparse attention to determining the spider hosts attacked by these fungi. In part, this has undoubtedly been due to a dearth of arachnologists whose services can be called upon to give a positive indentification. This poor inter-disciplinary collaboration is evidenced by the absence of any reference to fungal pathogens in published works on the biology of spiders, even when natural enemies are discussed (Foelix, 1982; Nentwig, 1986).

There is abundant circumstantial evidence, both from field observations and from analogy with closely-related insect fungi, to support the statement that most, if not all, of the fungi included here, can be implicated directly in spider mortality. The cuticle of spiders is essentially similar in composition to that of insects (Foelix, 1982). Nevertheless, the hard exocuticle, characteristic of insect exoskeleton, is not present in the abdominal region (opisthosoma) of spiders. Physically, therefore, the opisthosoma must be considerably easier for fungal spore penetration than the remaining spider exoskeleton, or compared to that of insects. Invariably, this is the part of the spider which first becomes mummi-fied and which later bears most of the external fungal mycelium and fructifica-tions. It is suggested that the majority of fungal infections take place through the spider abdomen, involving both mechanical and enzymatic penetration, and that the fungus once inside the haemocoele enters a yeast phase which subsequently produces a toxin lethal to the spider host. A review of fungal pathogenesis in insects can be found in Samson et al. (1987). There is no reason to believe that the process is significantly different in spiders.

The following is an account of the history, taxonomy and ecology of the fungal pathogens of spiders: the first of its kind, although a few papers relating specifically to descriptions of fungi on spiders have been published (Mains, 1950, 1954; Kobayasi & Shimizu, 1976). It is not intended to be a comprehensive review. The list of references has been pruned as far as possible, without hindering the more committed reader from gaining access to the 60-70 specialist taxonomy references con-sulted during the preparation of this article.

HISTORY

That spiders are subject to lethal fungal infections has been known for some con-siderable time. Gray (1858) described several entomopathogenic fungal species and indicated that both the adult and egg stages may be attacked. According to Petch (1932), the first illustration of a fungus on a spider host was by Ditmar

in 1817. This is reproduced in Gray's publication and the same species (*Akanthomyces aranearum*, see Fig. 7) was redescribed by Cooke (1892), in his masterly treatise on entomogenous fungi. For a more detailed insight into the subject, however, we are indebted to the industriousness of T Petch who named and described a large number of fungi from spider hosts. E B Mains made a shorter but no less effective contribution to our knowledge of these specialised
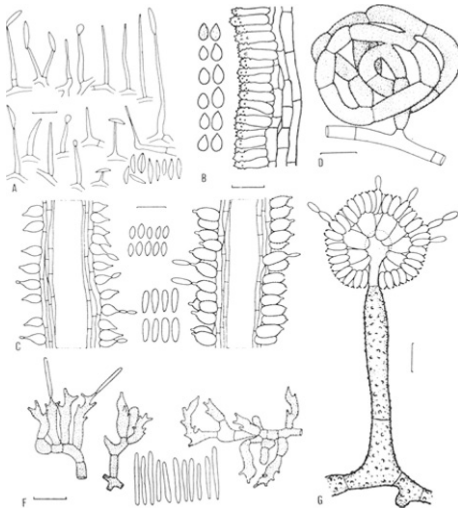

Fig. 1. Fungal genera on spiders. (A) *Hirsutella*; (B) *Hymenostilbe*; (C) *Akanthomyces*; (D) *Clathroconium*; (E) *Gibellula*; (F) *Granulomanus*. (Bar = 10um).

fungi, whilst Y Kobayasi, has had a long association with fungal pathogens of spiders which began more than 40 years ago with his classic monograph (Kobayasi, 1941) and has continued virtually to the present day (Kobayasi & Shimizu, 1983). Recent observations made by us on material collected in tropical ecosystems over the past 15 years, indicate that there are many species, and possibly genera, still to be described and even more awaiting discovery.

TAXONOMY

Significantly, perhaps, there are no known representatives of the lower fungi (Mastigomycotina) or the higher fungi (Basidiomycotina) attacking or actively parasitising spiders. There are records of such fungi, sometimes with araneogenous epithets, on spider hosts in the mycological literature but these appear to be either secondary colonisers of spider cadavers or hyperparasitic on obligate fungal pathogens. The Entomophthorales, for example, are commonly reported on most groups of terrestrial arthropods but, seemingly, have never been described from spiders. Indeed, the true pathogens are restricted to members of the Clavicipitales, and their hyphomycete anamorphs, which have developed mechanisms enabling them to invade, kill and colonise both insect and spider hosts. Some genera and species occur only on spiders whilst others are less selective in their host range. The following genera have been recorded on spiders and are either consistently or uniquely associated with these hosts:

Ascomycotina, Clavicipitales

Cordyceps (Fr.) Link (Figs. 3-4)
At least eight species have been confirmed on spiders (Kobayasi, 1941, 1982; Kobayasi & Shimizu, 1976, 1983; Mains, 1954).

Torrubiella Boud. (Figs. 2D, 5)
Twenty-seven species have been described from spider hosts (Kobayasi, 1982; Kobayasi & Shimizu, 1983).

Deuteromycotina, Hyphomycetes

Akanthomyces Leb. (Figs. 1C, 7)
Three species reported so far from spiders; both *Cordyceps* and *Torrubiella* teleomorphs have been proposed for two of these species (Samson & Evans, 1974).

Clathroconium Samson & Evans (Fig. 1D)
Monotypic genus, only on spiders; telemorph unknown (Samson & Evans, 1982).

Engyodontium de Hoog (Fig. 2C)
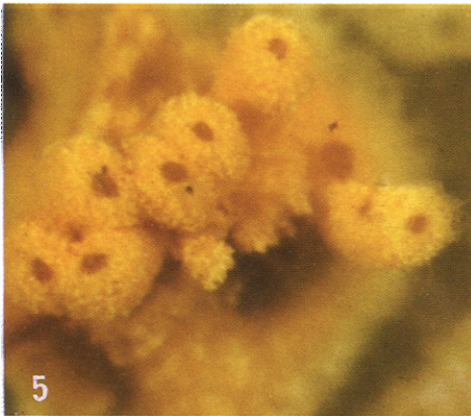Three species on spiders; *Torrubiella* teleomorph reported (Gams *et al.*, 1984).

Fig. 3. *Cordyceps caloceroides* on *Mugale* spider, Brazil. Fig. 4. *C. cylindrica* on trapdoor spider hidden in tunnel nest, Brazil. Fig. 5. Perithecia of *Torrubiella* sp. on small salticid spider, note orange ostioles emerging from yellow mycelial weft around perithecia, Ecuador. Fig. 6. Close-up of ostiolar region with emergent capitate asci.
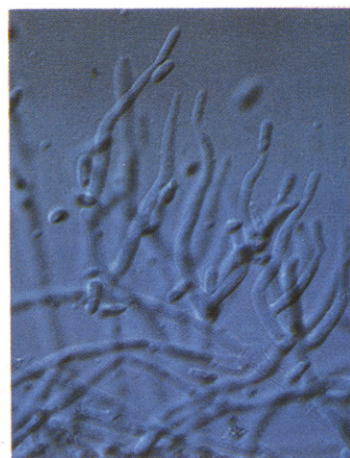
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Fig. 7. *Akanthomyces aranearum*, Ecuador. Fig. 8. *Hymenostilbe* sp. on salticid spider, Brazil. Fig. 9. *Granulomanus* synanamorph of *Gibellula* sp., Sulawesi. Fig. 10. *Verticillium* anamorph from ascospore culture of *Cordyceps caloceroides*, Brazil.

Gibellula Cav. (Figs. 1E, 11-17)
Four species validated, genus confined
to spider hosts (Petch, 1932; Mains, 1950;
Samson & Evans, 1973; Kobayasi, 1982;
Kobayasi & Shimizu, 1983). Synana-
morph: *Granulomanus* de Hoog & Sam-
son (Fig. 1F).

Hirsutella Pat. (Fig. 1A)
One authenticated species (Evans & Sam-
son, 1982) but Kobayasi & Shimizu (1976)
mention a *Hirsutella* anamorph when
describing a new *Cordyceps* taxon from
spiders.

Hymenostilbe Petch (Fig. 1B)
Two species reported to attack spiders;
teleomorph connection unproven (Sam-
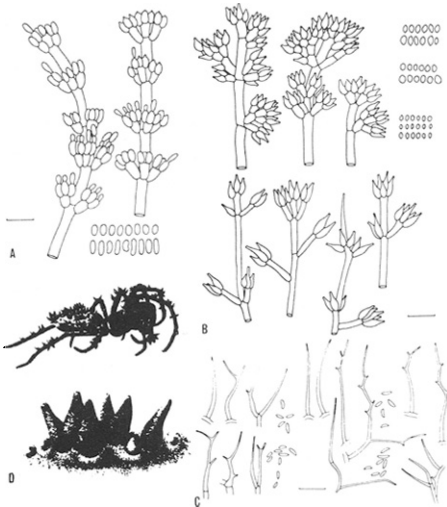son & Evans, 1975).

Fig. 2. Fungal genera on spiders. (A)
Nomuraea; (B) *Paecilomyces*; (C) *Engyodon-
tium*; (D) *Torrubiella* (ex M E Boudier, 1885).

Nomuraea Maubl. (Fig. 2A)
One species only but common on spiders
(Kobayasi, 1941; Samson, 1974); *Cor-
dyceps* teleomorph now confirmed
(Evans, 1982).

Paecilomyces Bain. (Fig. 2B)
Two species associated with spiders
(Samson, 1974); teleomorph probably in
the genus *Cordyceps*.

Verticillium Nees per Link (Fig. 10)
Two species recorded on spider hosts
(Gams, 1971), but several of the
araneogenous *Cordyceps* species have
been shown to produce *Verticillium*
anamorphs in culture (pers. obs.).

It is surprising that some of the
plurivorous, cosmopolitan insect
pathogens, such as *Beauveria bassiana*
(Bals.) Vuill. and *Metarhizium
anisopliae*(Metsch.) Sorok., are not more
common on spider hosts. The complete
absence of any spider pathogen in the
Entomophthorales is intriguing.

In the genus *Torrubiella*, the promi-
nent perithecia develop directly on the
spider cadaver, typically on the abdomen
and buried to some extent in a dense, fre-
quently brightly-coloured mycelium. As
in most of the fungi included here, the
mycelium also extends onto the substrate
helping to fix the spider in position. The
perithecia in the genus *Cordyceps*
develop on aerial structures (stromata).
The associated anamorph can occur
directly on the mycelium or on syn-
nemata of varying complexity.

ECOLOGY
Most of the fungal-infested spider
specimens examined by the authors have
been from subtropical and tropical forest
ecosystems and this reflects the richness
of these habitats as sources of entomo-
pathogenic Clavicipitales (Evans, 1982).
The diseased spider hosts are usually
found on the undersides of lower storey
shrubs and herbs, but occasionally on
tree boles. Most are free-living adult
spiders (possibly Salticidae), although
clutches of eggs and smaller spiders, en-
cased in tough silken threads or bags, are
also subject to attack. The larger forms
(Mygalidae) occur in the leaf litter or
buried in the soil in their silk-lined tun-
nels. There is evidence that tropical orb-
weaving spiders of the genera *Argiope*
and *Nephila* (Araneidae) are also infected
by pathogenic fungi, especially by
Nomuraea atypicola (Yasuda) Samson,
dying in their webs or nearby on abnor-
mal reduced webs (W Nentwig, pers.
comm.). The latter fungus has an in-
teresting host range since it is also

prevalent on large trapdoor spiders in Japan (Kobayasi, 1941), producing elaborate synnemata on the subterranean hosts. Synnematal function in *N. atypicola* is clear cut. In *Gibellula* it may be two-fold: improving dispersal efficiency by lifting the conidiophores into a more exposed position, thereby taking advantage of any air movement; augmenting sporulation capacity, particularly on small spiders, by increasing the spore-bearing area through complex branching. The apparent success of *Gibellula* as a spider pathogen may also be due to its ability to diversify its resources. The *Granulomanus* synanamorph could be directed at potential spider hosts coming into physical contact with the infected cadaver, rather than for aerial dispersal. However, movement of inoculum within the ecosystem is a speculative subject since we have no information on how and when the various types of spiders become infected.

Evans (1974) regularly recorded entomopathogenic fungi on spiders in forest habitats in Ghana. Six collecting sites (20m^2) were sampled monthly over a one-year period and, after ants and coccids, spiders were found to be the group of arthropods most affected by fungal pathogens. Over 150 specimens, representing 15 species in 10 genera, were collected. Samson & Evans (1973) also recorded high levels of spider mortality in Ghanaian cocoa farms, collecting 82 specimens of *Gibellula pulchra*(Sacc.) Cav. from 10 sample trees. Petch (1932) reported the same fungus as common at lower (tropical) altitudes in Sri Lanka. Another species of *Gibellula*, as yet undescribed, was collected in epizootic proportions over several years in Ecuadorian cocoa farms. A more recent survey was carried out in a monsoon forest habitat in the Far East (Sulawesi, Indonesia) and, out of a total of 690 fungal-infected arthropods, gathered during a three-week visit, 137 were spider hosts, or approximately 20% of the collection. Members of the genus *Gibellula* were especially well represented and this island seems to be a centre of diversity of these specialised spider pathogens (H C Evans, Unpubl.). Although it has not been possible to quantify the data further, spider populations are at a low level in most undisturbed tropical forests. It is concluded, therefore, that fungal pathogens constitute a significant spider mortality factor in such ecosystems. This is not to say that such fungi are rare or absent in other, less humid, temperate regions. Leatherdale (1958), for example, lists 13 species of fungal pathogens on spiders in the UK. The predominantly temperate Asian collections of Kobayasi (1982) and Kobayasi & Shimizu (1983), furthermore testify to their ubiquitousness.

It is now becoming increasingly apparent that spiders are an important component in the biological control of pest insects. Are fungal pathogens of spiders, therefore, a negative component in terms of pest control? Several arguments for and against can be put forward. Spiders do prey on pests and, consequently, any mortality factor of arachnids must be looked upon as detrimental to the crop and hence to man. Nevertheless, spiders are also natural enemies of beneficial insects and can destroy large numbers of insect predators. Moreover, they also compete with the latter for prey. Whichever argument is valid, and it could be either given the complexity of tropical crop ecosystems, the status of fungal pathogens should be carefully evaluated in any modelling of spider population dynamics.

There seems to be no better way of ending this article than by drawing upon the still relevant remarks from one of the earliest reviews on entomopathogenic fungi: "It is hoped, in conclusion, that these pages may awaken some curiosity, if not interest, in favour of these singular productions, and thus lead to further inquiry as to the species of insects that unfortunately become the bases of the fungoid parasites" (Gray, 1858).
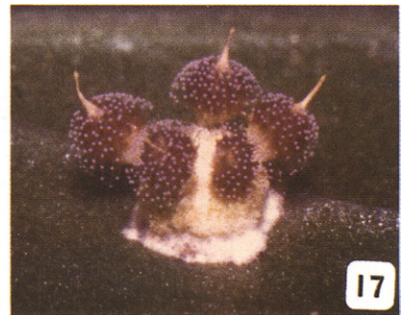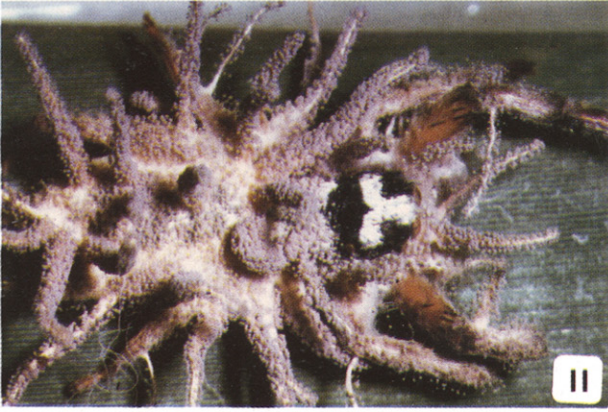
Figs. 11-17. Variations on a theme — the genus *Gibellula*. Fig. 11. *Gibellula leiopus*, sugarcane spider, Trinidad. Figs. 12-17. Undescribed *Gibellula* spp. on small, free-living salticid spiders from tropical forests.

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